COMPARATIVE VARIABILITY OF DRONES AND WORKERS OF THE HONEY BEE.[1]

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INTRODUCTION.

According to the theory of germinal variation it would be concluded that the workers of the honey bee, *Apis mellifica*, being produced from fertilized eggs, would show more variation than would the drones which come from parthenogenetic eggs. This variation would be manifested by coloration and by relative size of parts, and it might be expected that a series of measurements made on like parts of drones and workers would show a smaller degree of variability for drones than for workers. To test this fact a series of measurements have been made and the results tabulated.

Owing to the difficulty of measuring the extent of coloration on the segments of the abdomen this could not well be used for this work, and so a series of measurements on the wings were chosen although coloration is practically the only difference usually observed between the varieties of *Apis mellifica*.

The wings are also desirable for other reasons. They are of classificatory importance in systematic work, do not shrink when preserved in alcohol and are easily examined with a microscope by simply clipping off the wing and mounting in alcohol on a slide. They also give more accurate results since the extent of coloration would vary according to the retraction of the segments of the abdomen in preserving and it would be practically impossible to get the individuals normally extended in all cases.

The reason for taking up this work was rather indirect and should perhaps be stated since the results throw some light on a widely separated line of work. Perez[2] (1878) took an Italian queen fertilized by a French black drone, and after some time examined 300 drones from this queen. As the queen was pure

[1] Contribution from the Zoölogical Laboratory of the University of Pennsylvania.

[2] Perez, J., "Mémoire sur la ponte de l'abeille reine et la théorie de Dzierzon." *Ann. Sci. Nat.*, 6 Sér., Zoöl., T. 7, 1878.

Italian her drones would also be pure Italian, since they are produced from parthenogenetic eggs, and the fact that she was mated with a black drone should make no difference. He found, however, that 149 of the drones did show some markings which he thought indicated hybridism, and from these observations rejected the theory of Dzierzon. His results were criticised severely and all manner of arguments were used against them, atavism, impurity of the queen and other reasons being given in explanation. Weighing the arguments of Perez and those presented in opposition to them, however, would lead one to believe that Perez had the best of the argument. If then we accept the theory of Dzierzon, and it is well established, we must account for the results of Perez.

An examination of a large number of hives has shown us that the coloration of the drones cannot be used as a test of their purity, and that, therefore, Perez' work is inaccurate, since he used this test as the basis of his argument. Drones from an Italian queen fertilized by an Italian drone show gradations in amount of coloration of the segments of the abdomen which would easily lead one to conclude that some of them were not pure, provided the evidence for their purity was not so strong; while at the same time the workers from the same queen show a uniformity of marking which is very striking. In the face of these facts it is evident that extent of coloration could not be used as a basis for investigation in relation to parthenogenetic development in the case of the bee. It might also be added that the fact of the irregularity of coloration of the drones is well known to most bee-keepers, and a number of these men have stated to us that they do not consider the coloration of the drones as in any sense a test of purity.

This little investigation led to the conclusion that possibly the drones showed more variation in other ways than did the workers, and to test this the measurements here recorded were made.

We wish to express our appreciation to Mr. E. L. Pratt, of Swarthmore, Pa., for material furnished, and especially to Mr. E. R. Root, of Medina, Ohio, for material and for many courtesies shown during investigations carried on by one of us in his apiary.

Measurements.

For the measurements taken in this work we have chosen veins and cells which in the bee differ from the typical hymenopterous wing and which are to a certain extent typical of the bee in their direction and extent. In this choice we have followed the discussion of the venation of the Hymenoptera of Comstock and Needham.[1] The measurements were: (1) Length of vein radius (R); (2) diagonal length of cell radius-four (R_4); (3) length of vein media-two (M_2); (4) length of medial cross-vein (m); (5) ratio between m and M_2, and (6) number of hooks or hamuli on the hind wing. An attempt was made to measure the angles formed by the union of veins radius-four (R_4) and radius-sector (Rs), and veins radius-five (R_5) and radius-sector (Rs), but on account of the difficulty of getting the exact angle at which the veins branch these measurements were discontinued through fear of inaccuracy. In all cases right wings

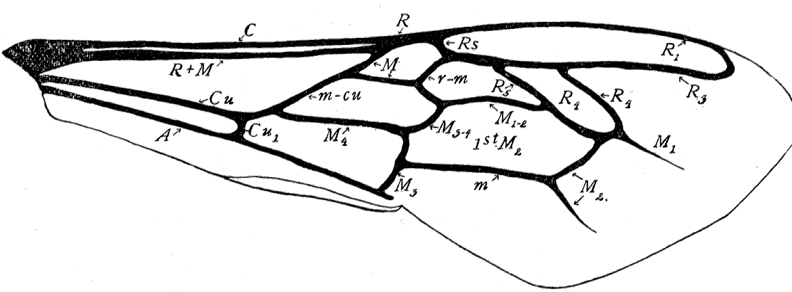

Fig. 1.

were measured. The measurements were made from camera-lucida sketches, Leitz ocular 2, objective 3 with lower lens removed and sketch made at table level, this giving a magnification of forty-two diameters. In all cases this magnification is retained in the tables.

The choice of the veins and cells measured perhaps needs some explanation since each one has certain peculiarities in direction or extent. It should be stated, however, that we do not think it makes much difference what veins are chosen for a comparison of variations in this case since all our observations show

[1] Comstock, J. H., and Needham, J. G., "The Wings of Insects," Chap. III. (continued), IX., "The Venation of the Wings of Hymenoptera." *Amer. Nat.*, Vol. 32, pp. 413–424, 12 figs., 1898.

about the same degrees of variability of the two sexes. Any other veins or cells would no doubt show like variations.

Length of Vein R. — In the typical hymenopterous wing the media (M) branches from the vein $R + M$ at a point nearer the base of the wing than in *Apis*. The length of the vein $R + M$ would therefore be desirable for measurement, but from the difficulty of getting exact measurements this was discarded, and in its place we took the measurement from the point where M branches off from $R + M$ to the point where R divides into R_1 and Rs or the length of R, which is therefore shorter than in the typical hymenopterous wing.

Diagonal Length Cell R_4. — In the typical hymenopterous wing veins R_4 and R_5 are nearly at right angles to the vein from which they branch, while in the bee, R_4 is bent out to about 135° and R_5 to 160°. This makes the cell R_4 considerably longer, and the diagonal length varies according as the angle $R_4 - Rs$ varies. The measurements were made from the proximal side of $R_5 - Rs$ to the anterior angle of $R_4 - M_1$.

Length of Veins M_2 *and* m. — In the bee's wing there is a bending in of the veins M_4 and M_3 toward the base of the wing with a corresponding lengthening and shifting of vein m. This vein gives a convenient measurement for the relative length of wing since it varies almost directly as the length increases. M_2 was chosen because it is correlated in its length with m, and forms a convenient relative measurement for the breadth of the wing.

Ratio between m *and* M_2. — As stated above, the lengths of m and M_2 are correlated in their variation, so in order to test the relative variabilities of the two veins in drones and workers, we computed the ratios between the two — $M_2 : m :: 1 : x$; x in every case being carried to two decimal places. From these computations it was found that the variation of m is in inverse proportion to that of M_2 as will be shown later.

Number of Hooks on Hind Wing. — This count was taken to see whether the hind wing varied as did the fore wing, and the number of hooks served as a conservative test.

Besides these measurements and calculations we looked for cases of abnormal wings in which the subcostal (Sc), radius-two (R_2) and cubital-two (Cu_2) veins might be present, these

being absent normally in the bee, and also for all other cases of abnormalities in the venation. In none of the wings observed were Sc, R_2 or Cu_2 present. The other abnormalities will be discussed later.

The Choice of Material.

The individuals used were not all taken from the same hive, since observations show that all colonies do not vary to the same extent, at least in coloration. For this reason it appeared best to use individuals from different hives and different strains in order to get a more correct idea of the natural variations. In all cases individuals were selected at random. The material used was as follows:

Drones.

I. Fifty individuals from Medina, Ohio, May 16, 1903. Hybrids, Italian and black.

II. One hundred individuals from Medina, Ohio, May 23, 1903. Italians (?) from a peculiar strain bred by F. A. Hooper, Jamaica, very light in color.

III. One hundred individuals from same hive as I. May 25, 1903.

IV. One hundred individuals from Medina, Ohio.

V. Fifty individuals from Medina, Ohio, May 9, 1903. Italians.

VI. One hundred individuals from Swarthmore, Pa., August 20, 1903. Italians from a peculiar strain bred by E. L. Pratt, the queen having an entirely yellow abdomen.

Workers.

I. Fifty individuals from same hive as Drones V., May 9, 1903.

II. Three hundred and fifty individuals from Philadelphia, Pa., August 10, 1903. Italians.

III. One hundred individuals from Philadelphia, Pa., May 15, 1902. Hybrids, Italian and black.

Length of Vein *R*.

The measurement of the length of this vein was found to be somewhat difficult owing to the hairs covering the angles and to the difficulty of getting the exact middle of the curve at the place where R_1 and Rs separate. However, with considerable care and

the reëxamination of cases showing the greatest variation we think the figures are nearly correct. Since the drones varied over 5 mm. on an average more than the workers and any error in measurement could scarcely be more than 1 or 2 mm. we feel justified in concluding that in this case the drones vary considerably more than the workers. The greatest variations were in Lot III. of the workers, where the variation was from 32 mm. to 42 mm., and in Lot VI. of the drones, where the variation was from 35 mm. to 48 mm. Lots I. of the workers and V. of the drones taken from the same hive at the same time show a range of variability in the ratio 8 : 11.

Table I.

Vein *R*.

Lot.	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	Av.
Drones.																				
I.					1	1	2	2	3	12	6	12	1	5	3	2				40.16
II.	1	1	1	7	8	22	19	21	11	6	3									35.99
III.					2	3	1	2	5	13	13	12	10	14	12	3	6	3	1	41.42
IV.	2	2	14	16	23	15	13	8	5	1	1									34.38
V.			1	3	3	5	11	8	7	5	3	3	1							36.92
VI.						3		9	11	18	14	10	14	8	8	3		1	1	40.42
	3	3	16	26	37	49	46	50	42	55	40	37	26	27	23	8	6	4	2	
Workers.																				
I.				2	1	3	4	11	17	9	3									37.46
II.					4	13	21	65	78	70	71	17	9		2					38.42
III.			1	1	5	11	10	26	19	12	10	2	3							37.40
			1	3	10	27	35	102	114	91	84	19	12		2					

Diagonal Measurement of Cell R_4.

This measurement being taken in one of the most variable regions of the wing shows a remarkable difference in the range of variability of the two sexes. The measurement of this distance was quite easy since the limits are well marked and easily distinquishable and in no case do we think there was room for doubt in the length to more than 1 mm. This fact taken with the length makes these measurements a very good test of the relative variability. In this region of the wing a very large part of the abnormalities were found, so that we conclude that this portion shows more variation than any other; but in spite of this tendency

to vary, the workers' wings were quite constant. The greatest range of variation in workers was found to be 13 mm., while the least range in drones was 19 mm. The fact that the average length of the cell in drones was between 96 mm. and 102 mm., while the average length for workers was about 75 mm., will however account for part of this greater range since, with a given range of variability, the greater the length, the less the actual variation. This, however, does not account for the extreme difference which we find and in this case again, as in the first set of measurements, we find a much greater variability in drones than in workers.

Table II.

Diagonal Cell R_4.

Drones.

Lot.	75[1]	80[1]	87[1]	89	90	91	92	93	94	95	96	97	98	99	100
I.				1			1		2	2	2	2	3	4	6
II.				1	2	6	10	9	6	10	6	5	9	8	13
III.							1		1		1	3		6	7
IV.					7	6	5	8	5	13	13	11	8	5	7
V.									1	2	1	3	1	5	4
VI.	1	1	1			1	1	2		12	11	4	6	12	13
	1	1	1	2	9	13	18	19	15	39	34	28	27	40	50

Lot	101	102	103	104	105	106	107	108	109	110	111	112	113[1]	115	Average.
I.	2	2	3	3	4	1	5	3	3	1					101.68
II.	9	4		1			1								96.49
III.	7	8	9	9	11	10	5	8	4	6	1	1	1	1	104.14
IV.	2	4	3	1	1			1							96.15
V.	3	6	6	8	4		2	3				1			101.98
VI.	11	6	8	2	3	2	1	1	1						98.77
	34	30	29	24	23	13	14	16	8	7	1	2	1	1	

[1] No individuals found in columns omitted.

Workers.

Lot.	69	70	71	72	73	74	75	76	77	78	79	80	81	82	Average.
I.	1	1	3	6	6	12	7	3	6	3	1	1			76.36
II.	1	10	18	20	42	37	71	62	38	24	16	4	4	3	75.08
III.		1	1	3	5	8	19	20	12	12	16	2	1		76.24
	2	12	22	29	53	57	97	85	56	39	33	7	5	3	

Length of Vein M_2.

This is not a specialized vein, and while it has for its anterior boundary the edge of the cell R_4, it shows comparatively little abnormality. A few cases of extra veins thrown in in the region of this vein will be discussed later, but it is located out-

side the portion of greatest abnormality of the wing. The principal reason for the measurement of this vein was to get a ratio with the vein m, but as the actual measurements add to the evidence, it seems advisable to give the table. The greatest range of variability in workers was 9 mm., the least for drones 11 mm., or, if we drop the two quite abnormal cases in Lot V., 9 mm. Taking into consideration the relative lengths of the average veins, 34 5 mm. and 45 mm., this makes the greatest variation in workers about equal to the least variation in drones, while the greatest range in drones is over twice that of the greatest range in workers.

Table III.

Vein M_2.

Drones.

Lot.	32	33	34	35	36	37	38	39	40	41	42	43	44
I.											3	2	
II.							6	8	12	6	21	16	17
III.													1
IV.			1							3	3	15	9
V.								2					4
VI.								1	1	2	1		2
			1				6	11	13	11	28	33	33

Lot.	45	46	47	48	49	50	51	52	53	54	55	56	Average.
I.	2		8	2	5	15	8	2	2	1			48.82
II.	6	5	2	1									42.26
III.	3	6	7	17	15	25	11	8	1	3	2	1	49.43
IV.	15	13	15	14	6	3	2	1					45.72
V.	8	5	6	10	11	2	1	1					46.96
VI.	2	3	7	11	14	13	10	15	13	2	3		48.64
	36	32	45	55	51	58	32	27	16	6	5	1	

Workers.

	32	33	34	35	36	37	38	39	40	
I.	7	12	19	9	1	2				33.82
II.	8	40	64	134	59	31	10	3	1	34.83
III.	4	10	42	22	10	11	1			34.61
	19	62	125	165	70	44	11	3	1	

Length of Cross-vein m.

This vein shows no abnormalities and may therefore be considered as entirely outside the region so well marked about the cells R_4 and R_5, which shows so much abnormal variation. If it be argued that, since the more anterior veins tend to be abnormal,

they are not therefore good tests of the comparative variability, then, since vein *m* is entirely outside this area, this measurement would serve as an answer to that argument and is in itself a sufficient test. As in the case of vein M_2, the measurements of this vein were made principally for the sake of getting a ratio of variation between two veins which meet at nearly a right angle, but as the drones show greater variation than the workers, although not to so great a degree as in some other cases, and as this is a constant vein, we add the table. The greatest range in workers is 16 mm., the least in drones 15 mm.; the average for workers almost 13 mm., the average for drones 20 mm.; the greatest for drones 23 mm. The average lengths in the two cases (72 mm. and 97 mm.) reduces this difference about one third, so that the least variable drones are about as constant as the least variable workers, but the average range for drones still remains considerably greater than for workers.

Table IV.

Vein *m*.

Drones.

Lot.	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
I.							1				1				1	3	3	1	6
II.										1			4	3	7	12	8	17	8
III.																		2	2
IV.	1		1		4	1	2	3	2	11	11	6	16	5	12	7	8	5	3
V.													2		2	3	4	2	4
VI.				1		1				1	2	2	5	5	6	10	12	14	13
	1		1	1	4	2	3	3	2	13	14	8	27	13	28	35	35	41	36

Lot.	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	Avg.
I.	1	4	2	7	5	2	3	3	3	4										100.04
II.	14	8	5	6	3	2	2													95.65
III.	4	9	5	16	4	12	8	11	10	4	2	4	2		2	1	1		1	102.43
IV.		2																		88.84
V.	9	13	1	3	2	3	1	1												97.08
VI.	6	7	7	5	2	1														94.63
	34	43	20	37	16	20	14	15	13	8	2	4	2		2	1	1		1	

Workers.

	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	Avg.
I.					1	2	2	4	6	13	7	8	4	2	1		72.30
II.	1			2	3	15	12	69	35	73	42	43	40	11	3	1	72.00
III.					1	2	1	10	16	18	27	13	8	2	2		72.43
	1			2	5	19	15	83	57	104	76	64	52	15	6	1	

Ratio Between M_2 and m.

To get this ratio the length of the vein m was divided by the length of the vein M_2 and the division carried to two decimal points giving a ratio in the form $M_2 : m :: 1 : x$. To get the comparative variability of the two sexes the individuals were tabulated according to the values of x and in this tabulation the values of x to *two* decimal points were used, but owing to the length of such a table we have combined these values and give them according to x carried to *one* decimal point. This is advisable also for another reason; owing to the relative smallness of the numbers in the first part of the proportion certain columns remained empty since, for example, no combination of figures between 32 and 57 and between 63 and 115 can give a ratio of 1 : 1.99. In order then to get a series of numbers which represents what is no doubt more nearly the true scale of ratios, the first table has been reduced to a table with x carried to but one decimal point. In tabulating these ratios the individuals were not grouped according to lots as in the other cases since we found practically little difference between the lots in any one sex. The average ratio for drones is 1 : 2.06 and for workers 1 : 2.08 so that no account need here be taken of the difference in averages since it is so slight. The range of the values of x for workers is from 1.70 to 2.34 or .64; that for drones from 1.68 to 2.90, or, omitting one wing with a very abnormal ratio, from 1.68 to 2.57 or .89 showing .25 greater range in drones than in workers. It might also be said, since our long table cannot be used here, that this greater range is not caused by a few abnormal cases but that the variations are shown by a gradually decreasing number of individuals in each value of x in both drones and workers, barring, of course, certain values of x which as above mentioned are impossible with the figures worked upon.

Table V.

Ratio Between M_2 and m.

Value of x.	1.7	1.8	1.9	2	2.1	2.2	2.3	2.4	2.5	2.6
Drones.	13	51	81	126	89	70	36	19	12	3
Workers.	1	11	53	119	217	81	17	1		

The working out of these ratios brought to light another point which explains this greater range in the values of x in the proportion. It was found that a certain inverse ratio exists between the lengths of m and M_2 so that the area of the cell $1stM_2$ bounded distally and posteriorly by these veins remains more nearly constant for wings of the same area than do the bounding veins. This does not mean that the area of the cell $1stM_2$ does not vary, for a little calculation shows that it does vary considerably. The ratios of the wings for each length of M_2 were gathered together and an average taken of the ratios in each case, with the result that we found a relatively constantly decreasing ratio with the increase in the length of M_2. The range of these ratios for drones was from 1.80 to 2.57, omitting again the one abnormal wing mentioned above, and for workers from 1.77 to 2.21, a difference in this case of .33 in the ranges of the two sexes. This would indicate seventy-five per cent. more range of variation for the drones than for the workers and this difference is directly correlated with the great difference in the size of M_2 found to exist.

TABLE VI.

RATIOS FOR LENGTHS OF VEIN M_2.

mm.	32	33	34	35	36	37	38	39	40	41	42	43	44
Drones.			2.05				2.57	2.43	2.35	2.25	2.28	2.16	2.14
Workers.	2.21	2.19	2.13	2.06	2.01	1.93	1.90	1.86	1.77				

mm.	45	46	47	48	49	50	51	52	53	54	55	56	Av.
Drones.	2.09	2.06	2.02	2.03	1.98	2.00	1.91	1.88	1.83	1.80	1.79	1.80	2.06
Workers.													2.08

HOOKS ON THE HIND WING.

The number of hamuli or hooks on the hind wing which are used to fasten the two wings together during flight were used as a means of testing the variability of this wing. The examination of 1,000 wings has shown that this is not the most variable feature of this wing, but that far more variation occurs in the breadth of the wing and in the angles of the veins which form the cross supports. As the area of the hind wing increases the increase takes place principally by a widening of the wing although by no means entirely by that method. The drones especially show

this widened wing, in some cases the width equalling the length. It may safely be stated, although no measurements were made on this point, that the area of the back wing is more variable than that of the fore wing. Since the number of hooks is correlated with the length of the wing they do not, therefore, show as much variation as would be found on the other parts of the hind wing. The least range of variation in number of hooks in workers was over seven points, the greatest, ten; the least for drones, nine, the greatest eighteen, or omitting one very abnormal wing with but twelve hooks, twelve. The relative amounts of variation are

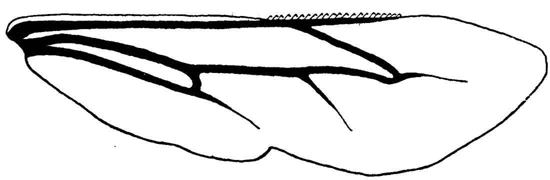

FIG. 2.

shown far more clearly here by examining the numbers of individuals in each case which have the same number of hooks. For the workers the greatest number is 139 individuals which have 21 hooks while for drones the greatest number is 98 with 22 hooks, the average number for drones being a little higher than for workers. In workers the descent in numbers of individuals from 21 is far more sudden than that for drones, which is really

TABLE VII.

HOOKS ON HIND WING.

	12	16	17	18	19	20	21	22	23	24	25	26	27	28	29	Avg.
Drones.																
I.				4	4	8	11	9	4	6	1	1	2			21.56
II.		2	1	12	21	23	20	17	2	2						20.12
III.				1	7	12	15	28	14	14	6	2	1			22.c9
IV.			4	10	17	22	27	12	2	5	1					20.33
V.				4	2	11	10	9	7	1	4	1		1		21.54
VI.	1			3	3	7	6	23	23	19	6	6	1		1	22.42
	1	2	5	34	54	83	89	98	52	47	18	10	4	1	1	
Workers.																
I.					6	9	12	11	6	5	1					21.42
II.			4	13	42	74	94	61	45	11	4	2				21.08
III.			2	11	18	18	33	8	6	4						20.37
			6	24	66	101	139	80	57	20	5	2				

the true test of the relative variability far more than is the range of variation.

So far we have discussed the range of variability in each case, but a far more important test of the comparative variability is the relative centralization of individuals about the average point in the table. If, for example, the drones showed exactly the same range as did the workers, the fact that in every one of the tables the workers show a greater number of individuals with the average dimensions, together with a rapidly decreasing number in each direction, while the drones show a more nearly equal number of individuals over several dimensions on each side of the average point, would lead one to conclude that the drones show far more variability than do the workers. It is not necessary to go over all the tables to point out this fact, but even a hurried examina-

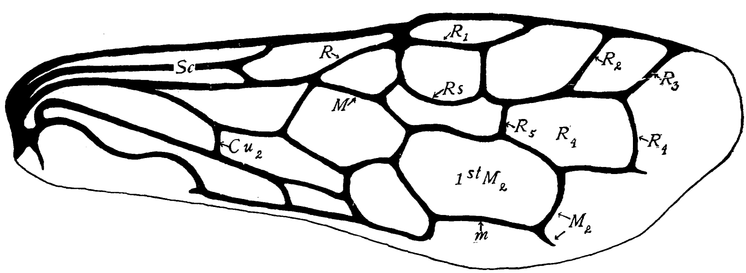

FIG. 3.

tion will show the facts as above stated. If, for example, the tables were put in the form of curves of variation the workers would show a longer and narrower curve in every case than the drones, and were these curves expressed in the form of mathematical formulæ the fact would be brought out still more strongly that the males in this case show more variation than do the abortive females.

It may be well here to offer some explanation as to why curves were not used in this work, since that is the usual method for work on variation. It was not the purpose of this investigation to work out the law of variation for the two sexes, but merely to show which sex did vary to the greater extent. This purpose has been fulfilled and is shown in the tables. In order to get a true curve of comparative variability it would be necessary to

measure many times the number of individuals which were used and to extend the observations over a far greater range of varieties. No curve made with 500 individuals would express the true law of variation, nor would ten times that number be sufficient, and since the formulation of the law of variation for parthenogenetic and fertilized forms for this particular kind of parthenogenesis, arrenotoky, is too important a matter to be based on an inaccurate mathematical formula, it seems better to us to state simply the fact that greater variation does occur in the males and leave the formulation of the law to be worked out with a far greater range of observations and measurements. And then, too, it is by no means certain that this variation follows any fixed law. If the variation were caused entirely by germinal variation, or by any other one factor, then it might be assumed that the law of this variation could be stated in the form of a mathematical formula, but as will be shown later, it appears probable that a large part of the greater variability of the drones is due to chance and is therefore not in accordance with any law. It may be argued that variation according to chance is but a way of stating our ignorance of the true law, but if there is a law for this variation it is certainly very obscure, and the working out of this law would require an extremely large number of measurements taken from individuals, each one with its life history known together with a high degree of mathematical ability in its formulation.

Abnormal Wings.

As noted previously, in all wings examined, record was made of wings having veins which are not typically found in the bee. Fig. 4 shows, in dotted lines, where these abnormalities occur most frequently. It is very difficult to record these irregularities in any kind of a table, since the irregular veins vary widely in extent and do not arise at exactly the same place in many cases. An attempt was made to classify these according to the veins from which they branch, their extent and direction. Manifestly any tabulation must be considered as merely a matter of convenience in examination. In this we have recorded cases where a vein bends (b in table) from its true course, showing but a tendency toward abnormality, as well as the well-marked cases. The ex-

tent of the abnormality is expressed roughly in the terms, very small (vs), small (s), almost complete (ac) and complete (c). The letters used to designate these abnormalities are in no way connected with the naming of the normal veins, but are chosen merely as a convenient means of marking the irregularities. It will be understood that it is impossible to draw at all times the same line between, for example, the terms small and very small,

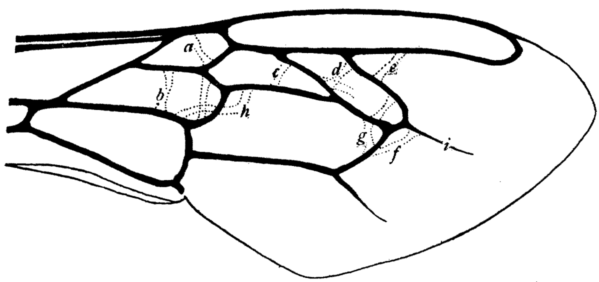

FIG. 4.

and the table is of no value except to give an idea of the number of cases of abnormalities.

	MALES.	FEMALES.
a.	82 b, 32 vs, 109 s, 1 ac, 2 irregular.	2 b.
b.	7 s, 1 double s, 4 ac, 6 c.	2 b.
c.	3 vs, 18 s, 2 ac, 13 c, 2 irregular.	1 b, 3 vs, 4 s.
d.	11 b, 27 s, 1 double s, 7 ac, 2 c.	3 b, 6 vs, 9 s.
e.	9 s, 1 ac, 5 c.	1 b, 1 vs, 3 s.
f, g.	8 irregular at anterior end.	2 irregular at anterior end.
h.	5 s, 2 c, 1 very irregular.	none.
i.	none.	2 lost veins; 1 almost lost.
Other irregularities, 14.		none.

Deducting the cases where more than one irregularity occurs on one wing we have 271 irregular drone wings and 37 worker wings. Leaving out of consideration those cases in which merely a bend is recorded there are 206 irregular drone wings and 30 irregular worker wings or almost seven times as many for drones as for workers.

The figure and these tabulations make clear what has been said previously about an area of irregularity in the wing. This region is rather well defined and no irregularities in venation were seen outside it.

A point which may well be recorded is that none of these veins

could be considered as in any sense mutations since there are in all cases varying degrees of abnormality indicating a gradual variation in the directions indicated.

No attempt has been made to correlate definitely these abnormalities with any lengths of the neighboring veins, but in a general way it can be said that the largest wings of each sex are the most abnormal, and this fact explains to some extent why the drone wings are so much more abnormal than those of the workers. From this it would appear that the cause of these abnormalities was the need of extra strengthening of the cells as they became larger, and that the irregularities are the result of extra growth energy, which has a chance to show itself when room is allowed for its manifestation.

Some Explanations of These Results.

With these facts before us it seems desirable to find, if possible, some explanations for these peculiar results. As stated in the introduction the theory of germinal variation would lead one to believe that the parthenogenetic individuals of the bee would show less variation than those from fertilized eggs and if there were no complicating factors it may be supposed that this would be true, but there are certain factors which modify this result so that the ratio of variation is exactly reversed.

In the first place that kind of parthenogenesis in which males only are produced (*arrenotoky*), is not such a specialized form of agamic reproduction as are those kinds of parthenogenesis in which females or both males and females are produced. When females only result from parthenogenetic eggs (*thelytoky*), a crossing of two lines of heredity seldom occurs and amphimixis can bring about little variation. In the case of the Aphids and Daphnids we have a similar condition except that once in a year or once in some life cycle males also are produced parthenogenetically and then there is an opportunity for the blending of hereditary traits through fertilization. To this last form of parthenogenesis the name *amphoterotoky* is applied. It is thus seen that in arrenotoky this mixing of hereditary traits is not dispensed with to such an extent as in the cases of thelytoky and amphoterotoky. On the other hand, the production of females par-

thenogenetically is of far more use to a species where gamic reproduction is unnecessary, since fertilization is not necessary to give a stimulus to the egg so that it may develop, and what the species loses in lack of cross fertilization is more than made up in the advantage it has through its parthenogenetic power. Since then arrenotoky is the least specialized form of parthenogenesis, and since a crossing does occur at every *second* generation in species with this power, it follows that according to the theory of germinal variation we would find more variation in arrenotoky than in either thelytoky or amphoterotoky. In fact the decrease in variability would not be very great, since in every case but one half the crossing is dispensed with.

Variation in parthenogenetic forms has been observed previously. Weismann[1] found that the parthenogenetic ostracod, *Cyprus reptans*, showed variation, and Warren[2] found considerable variation in Daphnids. Both of these cases fall under amphoterotoky, so that on *a priori* grounds we would expect still more variation in arrentoky. It is also held by some that males tend to vary more than females, and perhaps this tendency has something to do with what we find in the case examined. Davenport and Bullard,[3] found 2½ per cent. more variation in males than in females in swine. Darwin[4] gives a considerable number of cases showing the same tendency, and others have observed similar facts. On the other hand there are cases in the Odonata (*Gomphus* and *Macrothemis*, Calvert[5]) and in the Lepidoptera (*Thyreus abbotii*, Field[6]), in which the females are more variable than the males so that we must not assume too much on this ground.

This still leaves considerable variation in drones to be accounted

[1] Weismann, A., "The Germ-plasm," 1893.

[2] Warren, E., "An Observation on Inheritance in Parthenogenesis," *P. R. Soc. Lond.*, Vol. LXV., pp. 154–8, 1899.

[3] Davenport, C. B., and Bullard, C., "Studies in Morphogenesis," VI. "A contribution to the quantitative study of correlated variation and the comparative variability of the sexes." *Proc. Am. Soc.*, Vol. 32, pp. 85–97, 1897.

[4] Darwin, Charles, "The Descent of Man." London, 1871.

[5] Calvert, P. P., "The Odonate Genus *Macrothemis* and Its Allies," *Proc. Boston Soc. Nat. Hist.*, Vol. 28, pp. 301–332, 1898. "On *Gomphus fraternus*, *externus* and *crassus* (Order Odonata)," *Entomol. News*, March, 1901.

[6] Field, W. L. W., "A Contribution to the Study of Individual Variation in the Wings of the Lepidoptera," *Proc. Am. Ac. Sc.*, Vol. 38, pp. 389–396, 1898.

for and the following facts seem to us to help in this. The workers in a hive are hatched from cells one fifth of an inch in width and the size of these cells is remarkably uniform. On the other hand the drones hatch from cells which are generally one fourth of an inch in width, but often hatch in worker cells and from cells of all intermediate sizes. In the making of the comb under natural conditions there are a great many irregular cells formed which are transition cells between the worker and drone cells, and from these, if used for brood at all, drones are produced. It is true that sometimes a worker is produced in a drone cell, but this is very rare, provided there are any worker cells in the hive. Drone pupæ, on the contrary, are frequently seen in worker cells and are very noticeable on account of the exceptionally high arched cap which the workers put on when the larva is sealed up. This then gives to drones a greater amount of variation in the room provided for their growth while in the plastic state.

A bee larva will grow until it fills the cell in which it is placed and the young bee which emerges will be the size of the cell from which it came, within certain limits. This is shown in the production of queens by the modern methods of queen rearing used in apiculture. A young worker larva, less than one day old, is lifted from its cell and put into a cell cup of queen size. The workers complete this cup and form a queen cell and the larva in this cell grows to a much larger size than would be possible if it had remained in its original cell. Once in a while the bees will attempt to make a queen from a drone larva and while, of course, this is a failure yet the result is a very large drone. Generally, however, the drone under these conditions dies before reaching the imago stage. These facts show that the growth of an individual is limited by the size of the cell and also undoubtedly by the amount of food received during the unsealed larval stage. Then it follows that since the cells from which drones hatch vary from one fifth of an inch to over one fourth of an inch in width, while those from which workers hatch are quite uniform, that the variation in size will be considerably greater for drones than for workers.

This supposition is further strengthened by some of the facts

brought out by measuring the wings. Referring again to the table of the ratios varying according to the length of vein M_2 we find that the vein m varies *inversely* as the length of M_2. The length of vein m represents the ratio of the length of the wing while vein M_2 represents the ratio of the width. Probably most of the drones which have the shortest vein M_2 are those hatched from the smallest cells and the wings could not increase in width and therefore to meet the needs of the animal in making the necessary area of wing for flight the vein m must be lengthened. On the other hand, those drones hatched from the largest cells would be allowed greater room for the development of vein M_2 and vein m need not be so long.

Another fact which seems to indicate this is that those drone pupæ which are developing in worker cells are covered over by a very high cap, making the length of their cell much greater than that of the ordinary drone cell. The drones which hatch from these cells are long and narrow when compared with those from drone cells proper.

The drones in Lot II. were taken from a hive in which there were no drone cells except possibly a very few in the corners of the frame or near the top bar of the frame since all the combs were made on what beekeepers call foundation and the cells were uniformly of worker size. These drones show the least variation since they were all hatched under the same conditions. The drones of Lots I. and III. were hatched in old irregular combs and the tables show considerably greater variability.

The greatest number of abnormalities were found on the largest drone wings and the throwing in of extra veins is probably caused by the necessity for greater strengthening of the wings. Just how these extra veins arose is not easy to explain. They may be sports, or reversions to an ancestral type, or the result of extra growth-energy or caused by the splitting of normal veins so that it is rather difficult to say just what factors bring about this extra amount of variation. While we speak of these as abnormal veins it must be noted that we do not know whether they are really abnormal or whether they are but the manifestations of a tendency possessed by all bees but which can develop only under certain conditions, just as the ovaries of the workers can develop only when extra room and food are provided.

If then germinal variation will not explain all these variations and if we accept the explanation offered as a partial and possible statement of the cause, then it would appear that the mere chance as to which cell happens to be the receptacle of a drone egg determines its variation. While it is probable that even this "chance" is according to fixed law, the fact remains that in any event this law is beyond the possibility of formulation from any observations except those extending over far more individuals than those here used. On this account we consider ourselves justified in our tabulation of results rather than in the plotting of curves and expression in mathematical formulæ, since that would be undesirable except with far more measurements and with material gathered under conditions better controlled. Our tables show the variation as it actually exists in a state of nature and the real laws can be worked out only from observations from control experiments and this it is hoped will be possible in the near future.

We do not wish to be considered as advocating the inadequacy of the theory of germinal variation to explain variation, since we have no means of knowing whether these variations can be inherited but simply wish to express the facts as we find them, and leave the explanation of the bearing of germinal variation on this problem for future investigation.

October 1, 1903.

EXPLANATIONS OF FIGURES.

FIG. 1. Fore wing of honey bee, normal. Cells and veins are named according to Comstock and Needham.

FIG. 2. Hind wing of honey bee, normal.

FIG. 3. Typical hymenopterous wing according to Comstock and Needham.

FIG. 4. Part of fore wing of honey bee showing (in dotted lines) where accessory veins were seen to occur in the wings examined. Lettering purely arbitrary as explained in text.